THE GROWTH OF FOREST TREE ROOTS

W. B. McDougall

It has become a commonly accepted view that the growth of tree roots takes place in spring and in autumn, and that there is a period of rest in mid-summer as well as in winter. The workers who have published on this subject, however, do not all agree as to the time of year of the growth and rest periods, and no attempt seems to have been made by any of them to determine to what factor of the environment, if any, a summer rest period might be due.

Resa (1), who was the first to work intensively on the subject, came to the conclusion that deciduous-leaved trees produce their new roots in the autumn, while coniferous trees produce them in both autumn and spring, the exact time depending upon the weather. In the deciduous-leaved trees he found some root growth in the spring but not the formation of new roots. He also stated that the autumn growth period persisted, to a certain extent, throughout the winter, the period of root growth not corresponding at all with that of aerial growth. Wieler (2), on the other hand, found root growth only in the spring; but Petersen (3), Hämmerle (4), and Büsgen (5), all agreed with Resa that growth occurs in autumn as well.

Methods

The work on which the present paper is based was carried on in the "Forestry," a small artificial wood-lot at the University of Illinois. Two methods, or rather two modifications of one method, were used for making observations on the same roots at intervals throughout the growing season: (I) The horizontal glass-plate method. This method is similar to that used previously by the author (6) in making direct observations on developing mycorrhizas. The leaf mold and humus were scraped away to a depth of about two inches or until some healthy roots were exposed. These roots were then covered with a square of window glass, one foot square. Over this was placed a square of felt roofing and the whole was then covered with soil. The roofing kept the glass fairly clean but, nevertheless, it was

usually necessary to remove the glass when an observation was to be made. (II) The vertical glass-plate method. In order to make observations on roots located somewhat deeper than was possible by using horizontal plates, holes were dug in the earth two and one-half feet wide by five feet long and two feet deep. A glass plate, one foot square, was then placed against the soil and roots at one end of the hole in such a way as to exclude any extensive air spaces between the glass and the soil, and held in place by means of long pins made of number nine wire. A piece of felt roofing was placed against the glass to exclude light and was held in place by board props. The hole was then covered with a board cover hinged to two stakes at one side and locked with a padlock to a third stake at the opposite side.

Observations were made by both of the above methods on two individuals of each of the following four species of trees: *Acer saccharinum* L., *Tilia americana* L., *Carya laciniosa* (Michx f.) Loud., and *Quercus alba* L. The holes were dug and the glass put in place during December, 1913. They were first visited for observation on January 5, 1914, but regular observations did not begin until the twenty-eighth of April of that year. The work was continued until September 2, 1915. During the warmer parts of the year observations were made weekly except on two occasions, one in August, 1914, and one in July, 1915, when I was out of town for periods of two weeks. During the winter, observations were made usually only when the soil was not frozen. During the warmer part of the summer it was found that observations could not be made during the middle of the day without the roots being injured or killed by exposure to the warm dry air, especially on clear days. For that reason observations were regularly made just at or just after sunrise. In spite of this precaution many rootlets had their growth checked or even stopped permanently by exposure while observations were being made.

At each observation a chart of the observation field was made and the position of each fresh-looking rootlet was indicated thereon. At the same time the length of each rootlet was measured and recorded. Growth was recorded only when an increase in length could be detected in a week's time by measuring with an ordinary millimeter rule.

RESULTS IN 1914

Acer saccharinum: Growth had already begun at the time of the observation on April 28. At that time the leaves were about half developed. The trees were through blooming and the fruit, while still green, was nearly mature. The branches were growing rapidly.

The roots grew rapidly and many new rootlets were formed during May and June. June was a very dry month and July was still drier, so that by the middle of July we were in the midst of a pronounced drought. During the fore part of July the rate of root growth gradually lowered until by July 14 growth was almost at a minimum. This very slow rate of growth continued during the rest of July, often not more than a millimeter of elongation being detected in a week's time, and that only in a few rootlets. On August 6 growth had apparently entirely ceased and no further elongation could be detected during the remainder of August. The soil during this month was extremely dry. On August 28, however, it rained all day, and on September 8 growth had been resumed. During the remainder of September the roots continued to grow slowly. During the greater part of October no elongation could be detected, but on October 31 some growth was detected, and this continued until the end of November. No growth was detected after December 1. The month of December was very cold, being several degrees below zero during part of the time.

Tilia americana: The roots had already started growing on April 28. They grew rapidly during May and June, but after the first of July the rate of growth began to lower and by July 28 all elongation had ceased. On September 8 some growth was again detected, and the roots continued to grow slowly until November 24 after which no elongation was recorded.

Carya laciniosa: As in the above cases growth had already started on April 28, and continued through May and June. In July the rate of growth diminished and on July 28 it had ceased under both of the horizontal plates and under one of the vertical plates. Toward the bottom of the other vertical plate, however, the roots were still growing and they continued to grow unceasingly throughout the remainder of the summer. At no time, when an observation was made, was it found impossible to detect some elongation of these roots until after November 24. The roots under the other three plates had started

growing again on September 8 and continued to grow, though rather slowly, until November 24, after which no growth was recorded for any of the hickory roots.

Quercus alba: The first observations on the oak roots were made on May 5. At that time growth had already started. The roots grew rapidly until after the first of July and then slowly until July 28. On July 28 growth was recorded only in a single rootlet near the base of one of the vertical plates. No further growth was detected unti September 8 when it was noted that elongation had taken place in several roots under the vertical plates. These roots continued to grow during the rest of the season, but the first record of growth for roots under the horizontal plates was obtained on October 15. After this date there was growth under all of the plates until November 24, after which no further elongation was detected.

Results in 1915

The results in 1915 can be stated rather briefly. No observations were made on *Tilia americana*, during this year, for the reason that three of the preparations had been destroyed and a fungus had vegetated so freely under the fourth plate that it was considered useless to attempt further observation. For similar reasons observations were made on only one tree of *Acer saccharinum* instead of two.

The first observations for the year were made on March 23. At that time the flower buds of the soft maples were opening but no root growth was noted on either the maples, hickories or oaks. The first positive evidence of growth was obtained on April 5 on maple and hickory, and the first growth detected on the oaks was recorded on April 13. Warm spring weather began on April 5 and warm rains occurred on April 9 and 10. After April 13 the roots grew continuously as long as observations on them continued. At no time during the season when observations were made was it impossible to detect growth in the roots of all three species. The last observations were made on September 2 when the roots were still growing well. There was an abundance of rain throughout the season; there was no period of drought.

Tables I and II show in abbreviated form the data upon which the foregoing summary is based. It will be noted that the glass plates are designated by means of a numeral and a letter *A* or *B*. In every

case the numeral is the number given to the individual tree, while *A* indicates a horizontal plate and *B* a vertical plate. A + in the tables indicates that some elongation was observed in at least one root, while a — indicates that no growth was detected.

TABLE I

1914 Results

Date	*Acer saccharinum* Plates				*Tilia americana* Plates				*Carya laciniosa* Plates				*Quercus alba* Plates			
	1*A*	1*B*	2*A*	2*B*	3*A*	3*B*	4*A*	4*B*	5*A*	5*B*	6*A*	6*B*	7*A*	7*B*	8*A*	8*B*
Jan. 5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Apr. 28	+	+	+	—	—	+	—	+	—	+	+	+				
May 5	+	+	+	—	+	+	+	+	+	+	+	+		+	+	+
12	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
19	+	+	+	+	+	+	+	+	+	+	+	+	—	+	+	+
26	+	+	+	+	+	+	+	+	+	+	+	+	—	+	+	+
June 4	—	+	+	—	+	+	+	+	—	+	+	+	+	+	+	+
11	+	+	+	+	+	—	+	+	—	+	+	+	+	+	+	+
20	+	+	+	+	+	—	—	—	—	+	+	+	+	+	+	+
30	—	—	+	+	+	—	—	—	—	—	+	+	+	+	+	+
July 7	+	—	—	—	+	—	—	+	—	—	+	+	—	+	+	+
14	+	?	—	+	+	—	—	+	—	—	+	+	—	+	—	+
21	—	+	—	+	+	—	—	+	—	—	+	+	—	—	—	+
28	—	+	—	+	—	—	—	—	—	—	—	+	—	—	—	+
Aug. 6	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—
13	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—
29	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Sept. 8	+	+	+	—	+	—	—	+	+	+	+	+	—	+	—	+
16	+	+	+	+	+	+	—	+	+	+	+	+	—	+	—	+
19	+	+	+	+	+	+	+	+	+	+	+	+	—	+	—	+
29	—	—	+	+	+	+	—	—	+	+	+	+	—	+	—	+
Oct. 7	—	—	+	+	+	—	+	—	+	+	+	+	—	+	—	+
15	—	—	—	—	+	—	+	+	—	+	+	+	+	+	+	+
20	—	—	—	—	+	—	—	+	+	+	—	+	+	+	+	+
31	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Nov. 7	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
15	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
24	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Dec. 1	—	+	+	+		—	—	—	—	—	—	—	—	—	—	—
7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

DISCUSSION

The cause of periodicity in plants has been the subject of much discussion. Schimper (7) concluded from his own observations, and the observations of other workers in tropical regions, that plants in general of necessity show periodicity, and that this is due to internal causes. Klebs (8), on the other hand, brought forward considerable evidence against Schimper's interpretation and denied the existence

TABLE II

1915 Results

Date	*Acer saccharinum* Plates		*Carya laciniosa* Plates				*Quercus alba* Plates			
	2A	*2B*	*5A*	*5B*	*6A*	*6B*	*7A*	*7B*	*8A*	*8B*
Mar. 23.....	−	−	−	−	−	−	−	−	−	−
Apr. 5.....	+	+	+	−	−	+	−	−	−	−
13.....	+	+	+	+	−	+	+	+	−	+
20.....	−	+	+	+	+	+	+	+	−	+
26.....	+	+	+	+	+	+	+	+	+	+
May 8.....	−	+	−	+	+	+	+	+	+	+
17.....	+	+	+	+	+	+	+	+	+	+
25.....	+	+	+	+	+	+	+	+	+	+
June 3.....	+	+	−	+	+	+	+	+	+	+
12.....	+	−	+	+	+	+	+	+	+	+
12.....	+	+	+	+	−	+	+	+	+	+
26.....	+	+	+	+	+	+	+	+	+	+
July 5.....	+	+	+	+	+	+	+	+	+	+
20.....	−	+	+	+	+	+	+	+	+	+
27.....	−	+	+	+	+	+	+	+	+	+
Aug. 3.....	−	+	+	+	+	+	+	+	+	+
10.....	+	+	+	+	?	+	+	+	+	+
18.....	+	+	+	+	−	−	+	+	+	+
25.....	+	+	+	+	+?	+	+	+	+	+
Sept. 2.....	−	+	+	+	−	+	+	+	+	+

of periodicity independent of external factors. If the cause of a periodic phenomenon is internal, then, of course, there can be nothing gained by searching for a cause in the external environment. On the other hand, if the cause is external, then it is surely capable of being discovered, and, if an adequate cause is found in the external environment, then there is certainly no need of presupposing any mysterious internal factor.

Much evidence might be cited in support of the view that periodicity is due to external factors. It is well known that the resting period in various plants can be shortened by etherization or other means, and that many plants which, under natura conditions, have well-marked resting periods, may by artificial means be made to grow continuously. Appleman (9) has shown that the rest period of potato tubers is not of internal origin, but is dependent on external factors, the most important of which is the oxygen supply. According to Brown (10) the termination of the latent period in *Pinus strobus* is dependent upon three external factors; moisture, temperature and available reserve foods.

The results recorded in the present paper show conclusively that

the resting period of the roots studied are not fixed and hereditary, since, in 1914, although most of the roots under observation had a summer rest, some of the hickory roots did not have; and in 1915 there was no summer rest period in any of the roots studied, unless it occurred after September 1, which would be most unlikely. Therefore an external cause of the rest period, when it does occur, must be looked for. The two most important factors in the physical environment, that vary with the seasons, are temperature and moisture. A little study of the results given shows that the lowering of either the temperature or the moisture content of the soil retards or stops root growth. In 1914 there was very little rainfall from early spring until the end of August. The soil thus became progressively drier and reached a minimum of water content toward the end of August. The rate of root-growth also gradually decreased and ceased entirely in most cases some time in July, to begin again only after the heavy rains of August 28. In other words, the summer period of rest was only during the period of drought. In 1915 there was no period of drought and, naturally, no rest period. The hickory roots which did not have a rest period during the summer of 1914 were some of the most deeply located roots upon which observations were made, and, naturally, the soil was not so thoroughly dry at that depth as nearer the surface. It is probable that observations on still deeper roots would show all roots located where adequate moisture was available growing throughout the period of drought. Brown (10) found that in the aerial parts of the pine growth is retarded first in the upper portions of the tree and may continue for several weeks longer below. It is very probable that in the subterranean parts a similar difference between the upper and lower portions would be observed on the approach of a critical season.

It seems reasonable to conclude, then, that the summer rest period, when it occurs, is due not to any inherent tendency toward periodicity but to a lowering of the water supply. As to the winter rest period, the results show a close relation to temperature. But temperature to a certain extent controls the water supply, since a lowering of the temperature renders absorption increasingly difficult and thus reduces the amount of physiological water. In this case, therefore, the rest period is due indirectly to temperature but more directly to a decrease in the available water supply.

Mycorrhizal relations

In a previous paper (6) I stated that ectotrophic mycorrhizas are formed in late summer and autumn. In the light of the present investigation it would seem that the time of formation would vary more or less with the season. Two conditions are necessary for the formation of mycorrhizas; the roots must be growing and the proper fungus must be present and in an active and receptive condition. In the season of 1912, when the above mentioned work on mycorrhizas was done, the spring was wet enough for root growth but the early summer was very dry, while from the latter part of July on there was again plenty of moisture. Since no mycorrhizas were formed in the spring it may be supposed that the second condition mentioned above, the presence of a suitable fungus, was not fulfilled. So little is at present known concerning the ecology of the mushrooms that cause mycorrhizas that it is perhaps idle to speculate on their condition and activities in the spring of the year, but it is known that mycorrhizas are produced largely by the later fruiting mushrooms rather than by the spring forms. Since the fruit bodies are usually produced soon after the fungi have become attached to roots, it is reasonable to suppose that they are not in a condition for mycorrhiza formation earlier in the season.

Three of the species of trees used in the present investigation produce ectotrophic mycorrhizas, the oak (*Quercus*), hickory (*Carya*) and linden (*Tilia*). The mycorrhizas of the oak are due to *Russula foetentula* Pk., those of the linden to *Scleroderma vulgare*, Fr., and those of the hickory probably to *Laccaria ochropurpurea* (Berk) Pk., though this last has not been definitely proven. In all of these cases no mycorrhizas were formed in the spring, but after the first of July mycorrhizas were formed whenever the roots were growing well.

Conclusions

1. The root growth of forest trees begins as early in spring as the soil becomes warm enough for absorption and ceases in autumn when the soil becomes too cold.

2. There is not necessarily a summer resting period.

3. When there is a summer resting period it is due to a decrease in the water supply and not to any inherent tendency toward periodicity.

Botany Department,
University of Illinois

LITERATURE CITED

1. **Resa, F.** Ueber die Periode der Wurzelbildung. Inaug. Diss. Bonn. 1877.
2. **Wieler, A.** Das Bluten der Pflanzen. Cohn's Beiträge zur Biol. 6: 101. 1893.
3. **Petersen, O. G.** Etudes sur les phenomenes vitaux des racines des Arbres, Bot. Centralbl. 75: 272. 1898.
4. **Hämmerle, J.** Ueber die Periodicitat des Wurzelwachsthums bei Acer pseudoplatanus. Funfsctück's Beitr. zur Wissen. Bot. 4: 150, 1901.
5. **Büsgen, G.** Einiges über Baumwurzeln, Allg. Forst. u. Jagd. Ztg. **77**: 273. 1901.
6. **McDougall, W. B.** On the Mycorhizas of Forest Trees. Am. Jour. Bot. **1**: 51. 1914.
7. **Schimper, A. F. W.** Pflanzengeographie. 1898.
8. **Klebs, G.** Willkürliche Entwickelungs-Änderungen. 1903.
9. **Appleman, C. O.** Study of Rest Period in Potato Tubers. Maryland Agr. Exp. Sta. Bull. 183.
10. **Brown, H. P.** Growth Studies in Forest Trees. 2. Pinus strobus L. Bot. Gaz. **59**: 197. 1915.